

**LIFE HISTORY AND DESCRIPTION OF IMMATURE STAGES OF
NEASPILOTA APPENDICULATA FREIDBERG AND MATHIS (DIPTERA:
TEPHRITIDAE) ON *MACHAERANTHERA CANESCENS* (PURSH) A. GRAY
(ASTERACEAE) IN SOUTHERN CALIFORNIA**

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Abstract.—*Neaspilota appendiculata* Freidberg and Mathis is a univoltine, monophagous fruit fly (Diptera: Tephritidae) developing solely in the flower heads of *Machaeranthra canescens* (Pursh) A. Gray (Asteraceae) belonging to the subtribe Solidagininae of the tribe Astereae in southern California. The egg, first-, second-, and third-instar larvae, and puparium are described and figured. The pedicel of the egg is completely circumscribed apically by different sized, semicircular to elliptical aeropyles arranged singly and in rows of two to three parallel to the long axis of the egg. The dorsal sensory organ of the first instar is well defined, but flattened, not dome-shaped, and the single integumental petal and stomal sense organ are fused in this instar. The lateral stelex sensilla are ringed basally with three, irregular, poorly developed acanthae. The anterior thoracic spiracle of the second instar uniquely bears eight, cuboidal papillae, reduced to two or three, oblong papillae in the third instar. The ventrally-toothed oral ridges number seven in the third instar, which compares to seven or eight in one congener, and six in three other congeners examined to date. The ventrally toothed appearance and arrangement in a vertical series of these oral ridges appears to be a generic character. The puparium is reniform in shape. The larvae feed mainly on the ovules and soft achenes as first and second instars; however, as third instars, they usually extend their feeding into the receptacle and additionally feed on sap that collects in the shallow scars. The nonfeeding prepuparium overwinters in a protective cell that occupies much of the excavated flower head and is formed of floret, pappus, ovule and achene fragments impregnated with excess sap and liquid feces that harden when dry. A few prepuparia pupate and emerge from their cells in the late summer and fall and probably overwinter as adults, but most pupariate during the next year in late-winter to early spring, and emerge as adults that aggregate in summer on preblossom host plants to mate and subsequently oviposit. *Pteromalus* sp. (Hymenoptera: Pteromalidae) was reared as a solitary, larval-pupal endoparasitoid, and an unidentified Eulophidae (Hymenoptera) was reared as a gregarious endoparasitoid from puparia of *N. appendiculata*.

Key Words: Insecta, *Neaspilota*, *Machaeranthra*, Asteraceae, nonfrugivorous Tephritidae, biology, taxonomy of immature stages, flower-head feeding, monophagy, seed predation, parasitoids

Revision of the genus *Neaspilota* (Diptera: Tephritidae) by Freidberg and Mathis (1986) facilitated determination of specimens reared from California Asteraceae

(Goeden 1989) and stimulated several life-history studies, including those on *N. viridescens* Quisenberry (Goeden and Headrick 1992), *N. wilsoni* Blanc and Foote (Goeden and Headrick 1999), *N. signifera* (Coquillett) (Goeden 2000a), and *N. aenigma* Freidberg and Mathis (Goeden 2000b). This paper describes the immature stages and life history of a fifth species from California, *N. appendiculata* Freidberg and Mathis.

MATERIALS AND METHODS

The present study was based in large part on dissections of flower heads of *Machaeranthera canescens* (Pursh) A. Gray collected discontinuously during 1988–1997 mainly from the following three locations in the northern section of the San Bernardino Nat. Forest, SW San Bernardino Co.: Onyx Peak at 2700-m elevation, Caribou Creek along Van Duzen Canyon Road at 2120 m, and N shore Big Bear Lake at 2020 m. One-liter samples of excised, immature and mature flower heads containing eggs, larvae, and puparia were transported in cold-chests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. Six eggs, six first-, 12 second-, and 13 third-instar larvae, and five puparia dissected from flower heads were preserved in 70% EtOH for scanning electron microscopy (SEM). Additional prepuparia and puparia were placed in separate, glass shell vials stoppered with absorbant cotton and held in humidity chambers at room temperature for adult and parasitoid emergence. Specimens for SEM were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH and two, 1-h immersions in hexamethyldisilazane (HMDS), mounted on stubs, sputter-coated with a gold-palladium alloy, and studied and photographed with a Philips XL-30 scanning electron microscope in the Institute of Geophysics and

Planetary Physics, University of California, Riverside.

Most adults reared from isolated puparia were individually caged in 850-ml, clear-plastic, screened-top cages with a cotton wick and basal water reservoir and provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cages were used for studies of longevity and sexual maturation in the insectary of the Department of Entomology, University of California, Riverside, at $25 \pm 1^\circ\text{C}$, and 14/10 (L/D) photoperiod. Six pairs of virgin males and females obtained from emergence cages also were held in each of six separate, clear-plastic, petri dishes provisioned with a flattened, water-moistened pad of absorbant cotton spotted with honey (Headrick and Goeden 1994) for observations of their courtship and copulation behavior.

Plant names used in this paper follow Hickman (1993) and Bremer (1994); tephritid names and adult terminology follow Foote et al. (1993). Terminology and telegraphic format used to describe the immature stages follow Goeden (2000a, b), Goeden et al. (1998), Goeden and Headrick (1992, 1999), Goeden and Teerink (1997; 1998; 1999a, b), Teerink and Goeden (1999), and our earlier works cited therein. Means $\pm$ SE are used throughout this paper. Voucher specimens of *N. appendiculata* immature stages, adults, and parasitoids reside in my research collections.

RESULTS AND DISCUSSION

Taxonomy

Adult.—*Neaspilota appendiculata* was described by Freidberg and Mathis (1986, p. 37–39), who pictured the unpatterned wing (p. 72), along with drawings (p. 38) of the lateral aspect of the head, male right foretarsus, epandrium, distiphallus, epandrium and cerci, aculeus and its apex enlarged, and spermatheca.

Immature stages.—The egg, first-, second-, and third-instar larvae, and puparium

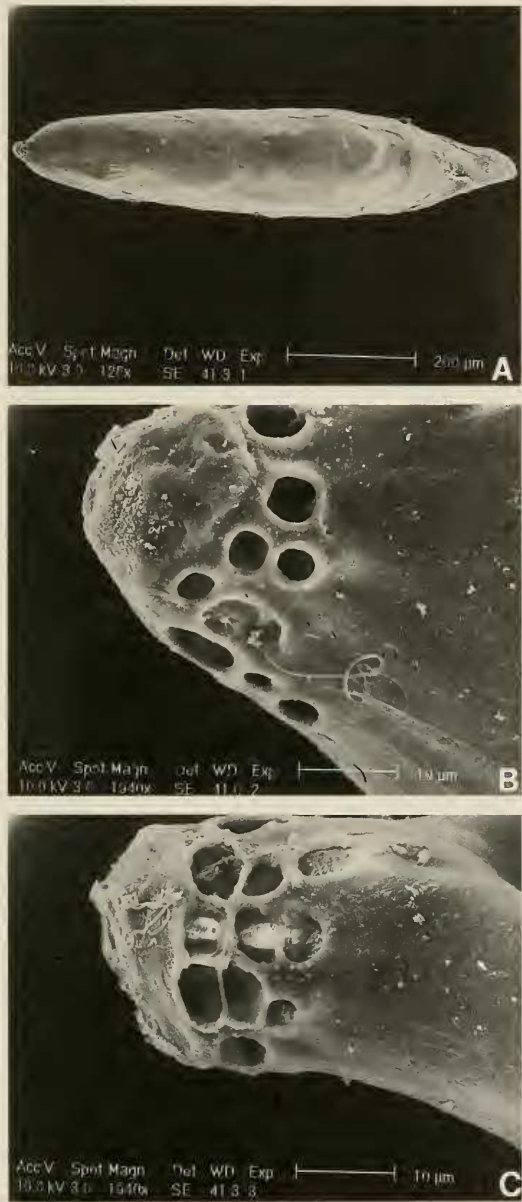


Fig. 1. Egg of *Neaspilota appendiculata*: (A) habitus, anterior end to left; (B) pedicel showing pattern of aeropyles; (C) pedicel of a different egg with its aeropyles.

heretofore have not been described or figured.

Egg: Thirty-three eggs dissected from field-collected flower heads were white, opaque, smooth, elongate-ellipsoidal, 0.71 ± 0.017 (range, 0.62–0.96) mm long, 0.175

± 0.003 (range, 0.16–0.22) mm wide, smoothly rounded at tapered basal end (Fig. 1A); pedicel button-like, 0.02 mm long, completely circumscribed apically by different-sized, semicircular to elliptical, shallow aeropyles, through which the spongy inner layers of the chorion are readily visible; aeropyles arranged singly and in rows of two to three, parallel to the long axis of the egg (Fig. 1B, C).

The egg of *N. appendiculata* is similar in shape to those of *N. viridescens* (Goeden and Headrick 1992) and *N. wilsoni* (Goeden and Headrick 1999), but about 20% longer on average than that of *N. viridescens*, and 24% shorter and 27% wider on average than that of *N. wilsoni* (Goeden and Headrick 1999). Moreover, *N. appendiculata* has more aeropyles that are more regularly and densely spaced around the pedicel apex than *N. viridescens* (Goeden and Headrick 1992), but fewer aeropyles than *N. wilsoni*, which essentially cover the conical pedicel (Goeden and Headrick 1999). The eggs of 12 species of *Trupanea* from California mainly differ from eggs of the three *Neaspilota* spp. studied to date by having pedicels circumscribed by only one or two rows of aeropyles (Goeden and Teerink 1999b and references therein).

First instar: White, elongate-cylindrical, bluntly rounded anteriorly and posteriorly (Fig. 2A); body segments well defined, nearly free of minute acanthae; gnathocephalon smooth, lacking oral ridges, with pair of prominent integumental petals dorsad of mouth hooks (Fig. 2B-1); dorsal sensory organ well-defined, dome-shaped papilla (Fig. 2C-1), pit sensillum at base of dorsal sensory organ; anterior sensory lobe (Fig. 2B-2, C-2) bears terminal sensory organ (Fig. 2C-3); lateral sensory organ (Fig. 2C-4), supralateral sensory organ (Fig. 2C-5), and pit sensory organ (Fig. 2C-6); stomal sense organ ventrolateral of anterior sensory lobe (Fig. 2B-3, C-7), integumental petal (Fig. 2B-1) fused laterally with stomal sense organ (Fig. 2B-3); mouthhook bidentate (Fig. 2B-4, C-8); median oral lobe lat-

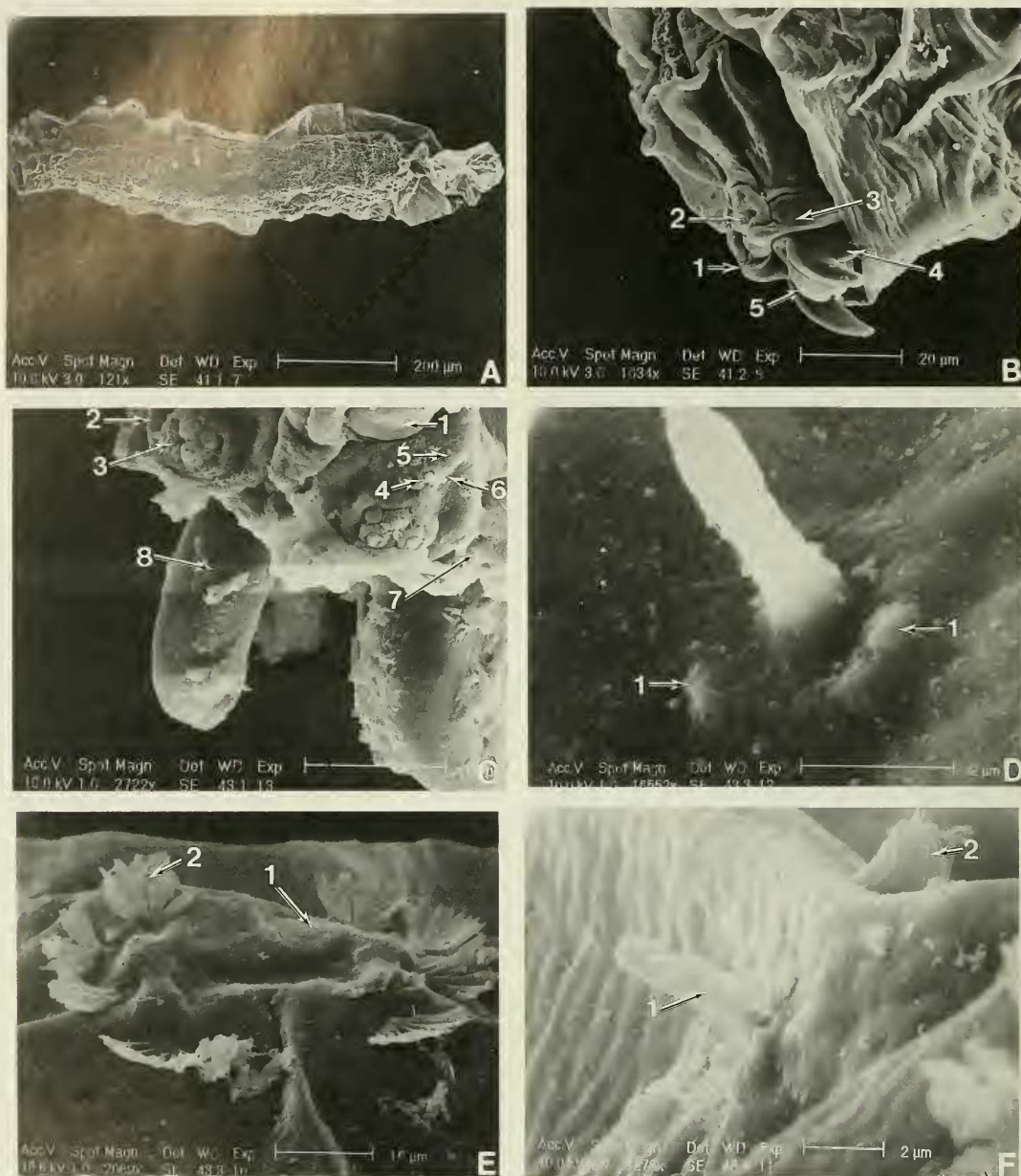


Fig. 2. First instar of *Neaspilota appendiculata*: (A) habitus, anterior to left; (B) gnathocephalon, ventrolateral view, 1-integumental petal, 2-anterior sensory lobe, 3-stomal sense organ, 4-mouth hook, 5-median oral lobe; (C) gnathocephalon, frontal view, 1-dorsal sensory organ, 2-anterior sensory lobe, 3-terminal sensory organ, 4-lateral sensory organ, 5-supralateral sensory organ, 6-pit sensory organ, 7-stomal sense organ, 8-mouthhook; (D) ventrolateral stlex sensillum, 1-basal acanthae; (E) anal segment, 1-rima, 2-interspiracular process; (F) intermediate sensory complex, 1-stelix sensillum, 2-medusoid sensillum.

erally flattened (Fig. 2B-5); meso- and metathoracic and abdominal lateral spiracular complexes not seen; caudal segment with two stlex sensilla, dorso- and ventro-

lateral of posterior spiracular plate, each stlex sensillum (Fig. 2D) basally ringed with three, irregular, poorly developed acanthae (Fig. 2D-1); posterior spiracular

plate bears two ovoid rimae, ca. 0.008 mm in length (Fig. 2E-1), and four interspiracular processes, each with two to four branches, longest measuring ca. 0.01 mm (Fig. 2E-2); intermediate sensory complex with one stelex sensillum (Fig. 2F-1) and one medusoid sensillum (Fig. 2F-2).

The first instar is similar in general habitus to that of *N. viridescens* (Goeden and Headrick 1992), *N. wilsoni* (Goeden and Headrick 1999), *N. signifera* (Goeden 2000a), and *N. aenigma* (Goeden 2000b). However, unlike *N. viridescens*, but like *N. wilsoni* and *N. aenigma*, the dorsal sensory organ of the first instar of *N. appendiculata* is well defined (Fig. 2C-1), as is the anterior sensory lobe (Fig. 2B-2, C-2) and integumental petal (Fig. 2B-1). Also, the pit sensory organ (fig. 2C-6), not seen in *N. viridescens* (Goeden and Headrick 1992) and presumably hidden in specimens viewed of *N. signifera* (Goeden 2000a), is present in *N. appendiculata*, as it is in *N. wilsoni* (Goeden and Headrick 1999) and *N. aenigma* (Goeden 2000b). A fused integumental petal and stomal sense organ also was reported in first instars of *N. wilsoni* (Goeden and Headrick 1999), *N. signifera* (Goeden 2000a), and *N. aenigma* (Goeden 2000b) as well as *Trupanea vicina* (Wulp) (Goeden and Teerink 1999b), but these structures were separated in *N. viridescens* (Goeden and Headrick 1992).

Having two stelex sensilla dorso- and ventrolaterad of each posterior spiracular plate in the first instar of *N. appendiculata* (Fig. 2D) and *N. aenigma* (Goeden 2000b) agreed with the four such sensilla reported to ring the caudal segment of *N. wilsoni* (Goeden and Headrick 1999), but not the 10 sensilla reported to ring the caudal segment of *N. viridescens* (Goeden and Headrick 1992). The last number is probably erroneous, as discussed by Goeden (2000b). Lateral stelex sensilla on the caudal segment that are basally ringed with acanthae (Fig. 2D-1) first were reported in *N. wilsoni* (Goeden and Headrick 1999), where the upright acanthae among them number one to

three and are pointed, and in *N. aenigma* (Goeden 2000b), where the upright acanthus is solitary and rounded apically.

Second instar: White, elongate-cylindrical, rounded anteriorly, truncated dorsoposteriorly (Fig. 3A), body segments well defined, circumscribed by only a few minute acanthae; dorsal sensory organ well-defined (Fig. 3B-1, C-1), with basally associated pore sensilla (Fig. 3C-2); anterior sensory lobe (Fig. 3B-2, C-3) with terminal sensory organ (Fig. 3B-3, C-4), lateral sensory organ (Fig. 3C-5), supralateral sensory organ (Fig. 3C-6), and pit sensory organ (Fig. 3C-7); stomal sense organ ventrolaterad of anterior sensory lobe (Fig. 3B-4, C-8); mouthhook bidentate (Fig. 3B-5); median oral lobe laterally compressed (Fig. 3B-6), ventrally transversely divided (not shown); seven papilliform, integumental petals dorsal to each mouthhook (Fig. 3B-7, C-9); six oral ridges toothed ventrally, lateral to oral cavity (Fig. 3B-8); pore sensilla circumscribe gnathocephalon posterior to oral ridges (Fig. 3B-9); prothorax circumscribed anteriorly by minute acanthae (Fig. 3B-10); anterior thoracic spiracle with eight cuboidal papillae (Fig. 3D); lateral spiracular complexes not seen; caudal segment with two stelex sensilla dorsolaterad and ventrolaterad of posterior spiracular plate (not shown); posterior spiracular plate bears three ovoid rimae, ca. 0.02 mm long, and four interspiracular processes, each with four, simple or forked branches, longest measuring 0.012 mm; intermediate sensory complex with a stelex sensillum and a medusoid sensillum.

The habitus of the second instar of *N. appendiculata* (Fig. 3A) is more like *N. wilsoni* (Goeden and Headrick 1999), *N. signifera* (Goeden 1999a), and *N. aenigma* (Goeden 2000b) than the barrel-shaped second instar of *N. viridescens* (Goeden and Headrick 1992). The dorsal sensory organ of *N. appendiculata* is well defined in the second instar (Fig. 3C-1), as with *N. signifera* (Goeden 1999a), but is not well defined in *N. viridescens* (Goeden and Head-

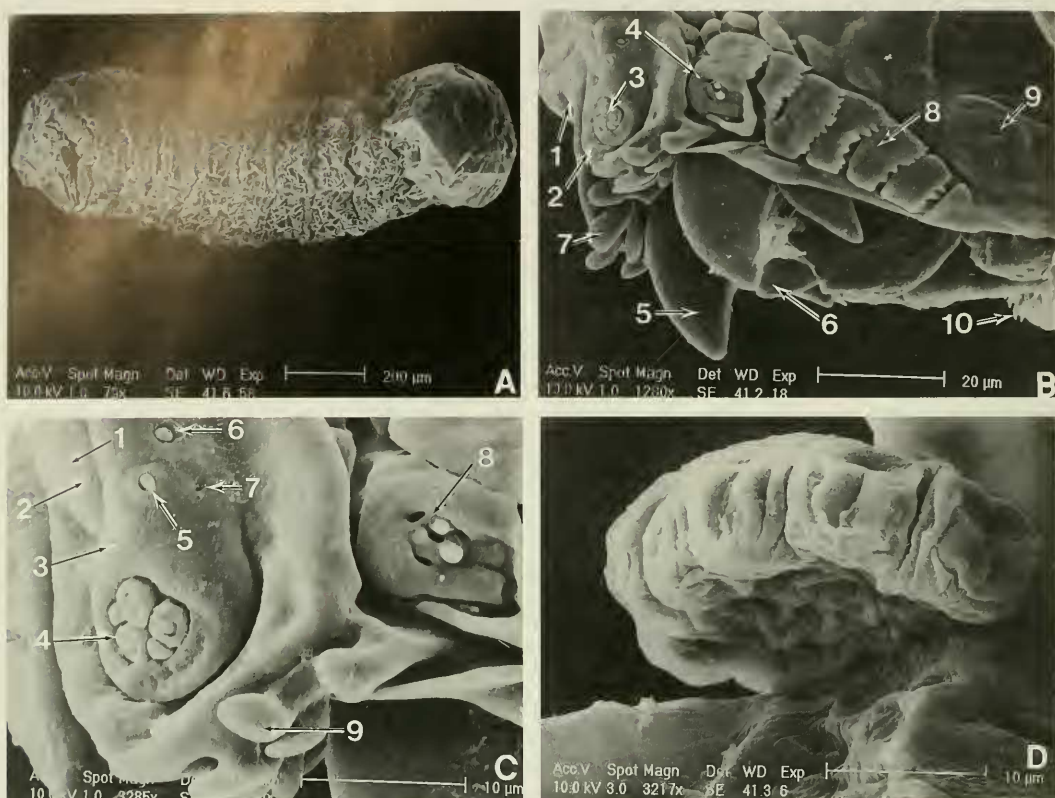


Fig. 3. Second instar of *Neaspilota appendiculata*: (A) habitus, anterior to left; (B) gnathocephalon, ventro-lateral view, 1-dorsal sensory organ, 2-anterior sensory lobe, 3-terminal sensory organ, 4-stomal sense organ, 5-mouthhook, 6-median oral lobe, 7-integumental petal, 8-oral ridge, 9-pore sensillum, 10-minute acanthae; (C) anterior sensory lobe, 1-dorsal sensory organ, 2-basilateral, pore sensillum, 3-anterior sensory lobe, 4-terminal sensory organ, 5-lateral sensory organ, 6-supralateral sensory organ, 7-pit sensory organ, 8-stomal sense organ, 9-integumental petal; (D) anterior spiracle.

rick 1992), *N. wilsoni* (Goeden and Headrick 1999), or *N. aenigma* (Goeden 2000b). The integumental petals of the second instars of all five species are papilliform and seven in number above each mouthhook in *N. appendiculata* (Fig. 3B-7), but four occur in *N. signifera* (Goeden 2000a), six in *N. viridescens* (Goeden and Headrick 1992), seven in *N. wilsoni* (Goeden and Headrick 1999), and eight occur in *N. aenigma* (Goeden 2000b); whereas, in the first instars of all five congeners examined these structures are broad, flattened, and paired (Fig. 2B-1; Goeden and Headrick 1992, 1999; Goeden 2000a, b). A clear difference in *N. appendiculata* is the eight papillae on the anterior spiracle of the second

instar (Fig. 3D), compared to three to four papillae in second instars of *N. viridescens* (Goeden and Headrick 1992), *N. wilsoni* (Goeden and Headrick 1999), *N. signifera* (Goeden 2000a), and *N. aenigma* (Goeden 2000b). Only the third-instar of *Paracantha gentilis* Hering with seven to eight papillae on the anterior spiracle (Headrick and Goeden 1990) approached this number among the 34 species of tephritid larvae that we have described in similar detail to date. Finally, the interspiracular processes each bear four branches, not one to four branches like *N. aenigma* (Goeden 2000b), nor two to four branches like *N. signifera* (Goeden 1999a), nor five to nine branches like those of *N. viridescens* (Goeden and Headrick

1992), nor two to six branches like those of *N. wilsoni* (Goeden and Headrick 1999).

Third instar: Pale yellow, with posterior spiracular plate dark brown to black, elongate-cylindrical, tapering anteriorly; posterior spiracular plate on caudal segment flattened and upturned dorsally ca. 60° (Fig. 4A), minute acanthae circumscribe anterior thirds of thoracic and abdominal segments (Fig. 4B-1, C-1, D-1); gnathocephalon conical (Fig. 4B); dorsal sensory organ a well-defined, circular, flattened pad (Fig. 4B-2); anterior sensory lobe (Fig. 4B-3) bears terminal sensory organ (Fig. 4B-4), lateral sensory organ (Fig. 4B-5), supralateral sensory organ (Fig. 4B-6), and pit sensory organ (not shown); six, papilliform, integumental petals above each mouthhook (Fig. 4B-7); seven oral ridges toothed ventrally lateral to oral cavity (Fig. 4B-8); stomal sense organ ventrolateral of anterior sensory lobe (Fig. 4B-9); mouthhook tridentate (Fig. 4B-10); median oral lobe laterally flattened (Fig. 4B-11); prothorax circumscribed by minute acanthae (Fig. 4B-1); verruciform sensilla circumscribe prothorax posteriorad of minute acanthae (Fig. 4B-12); anterior thoracic spiracle on posterior margin of prothorax bears two or three oblong papillae; mesothoracic lateral spiracular complex consisting of spiracle (Fig. 4C-2) and five verruciform sensilla (Fig. 4C-3), two above and three below the spiracle; metathoracic lateral spiracular complex consisting of five verruciform sensilla (Fig. 4C-4), one above and four below the spiracle (Fig. 4C-5); abdominal lateral spiracular complex consists of a spiracle (Fig. 4D-1) anterior to a verruciform sensillum (Fig. 4D-2), and two or three other verruciform sensilla, one above (not shown in Fig. 4D) and one (Fig. 4D-2) or two (unpublished data) below the spiracle; caudal segment circumscribed by minute acanthae (Fig. 4E-1); each posterior spiracular plate bears three ovoid rimae, ca. 0.03 mm in length (Fig. 4E-2), and three-four interspiracular processes (Fig. 4E-3), each with four, simple, pointed or forked branches,

longest branch measuring 0.015 mm; stelex sensilla (Fig. 4F) dorsolaterad, laterad, and ventrolaterad of posterior spiracular plate (Fig. 4E); each of the eight stelex sensilla surrounding the posterior spiracular plate in turn ringed by four to six, conical minute acanthae (4F-1); intermediate sensory complex with a medusoid sensillum and a stelex sensillum.

The habitus of the third instar of *N. appendiculata* generally is like that reported for *N. viridescens* (Goeden and Headrick 1992), *N. wilsoni* (Goeden and Headrick 1999), *N. signifera* (Goeden 2000a), and *N. aenigma* (Goeden 2000b). Like *N. signifera* (Goeden 2000a), the anterior part of each body segment of *N. appendiculata* is circumscribed by minute acanthae. Whereas, in *N. aenigma* the anteriors, pleura, and posteriors of each segment are thus circumscribed (Goeden 2000b); in *N. wilsoni*, all intersegmental areas and all abdominal segments except the pleura are so circumscribed (Goeden and Headrick 1999); and in *N. viridescens*, the intersegmental areas are free of acanthae (Goeden and Headrick 1992). Unlike *N. viridescens* (Goeden and Headrick 1992) and *N. wilsoni* (Goeden and Headrick 1999), but like *N. signifera* (Goeden 2000a) and *N. aenigma* (Goeden 2000b), the dorsal sensory organ is well defined, but flattened and not dome-shaped in the third instar of *N. appendiculata* (Fig. 4B-2). In the second instar of *N. wilsoni* (Goeden and Headrick 1999), *N. signifera* (Goeden 2000a), and *N. appendiculata* (Fig. 3B-2), the dorsal sensory organ is both prominent and dome-shaped, as it is in the first instar of all congeners except *N. signifera*, where it was hidden in my specimens and could not be examined for comparison (Goeden 2000a).

Additional similarities involved the integumental petals in the third instars of all five congeners examined to date, all of which are papilliform and arranged in a double row above each mouth hook (Goeden and Headrick 1992, 1999; Goeden 2000a, b; Fig. 4B-7). The stomal sense or-

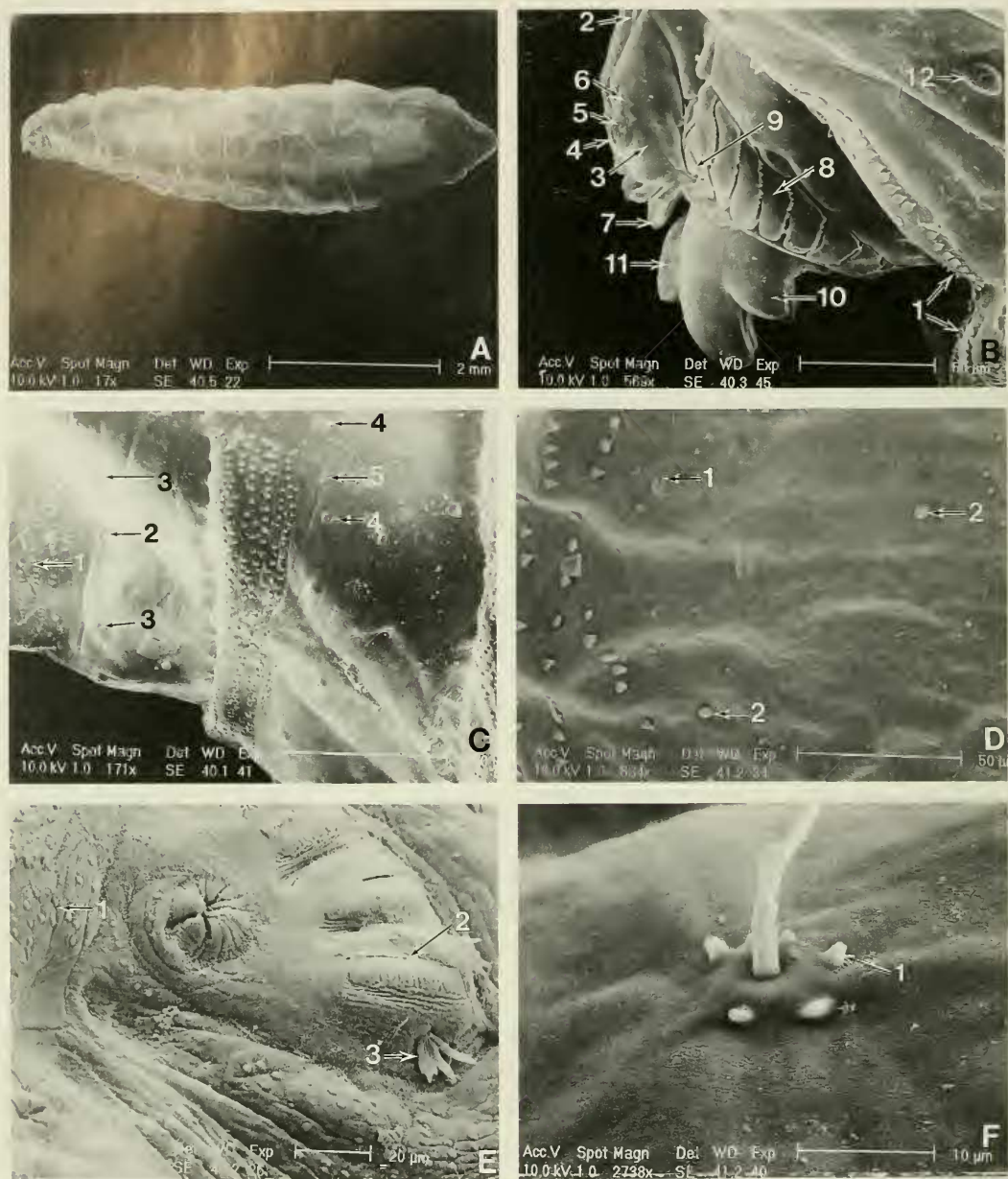


Fig. 4. Third instar of *Neaspilota appendiculata*: (A) habitus, anterior to left; (B) gnathocephalon, lateral view, 1-minute acanthae, 2-dorsal sensory organ, 3-anterior sensory lobe, 4-terminal sensory organ, 5-lateral sensory organ, 6-supralateral sensory organ, 7-integumental petal, 8-oral ridge, 9-stomal sense organ, 10-mouth-hook, 11-median oral lobe, 12-verruciform sensillum; (C) meso- (left) and metathoracic (right), lateral spiracular complexes; 1-minute acanthae, 2-spiracle on mesothorax, 3-verruciform sensillum of mesothorax, 4-verruciform sensillum on metathorax, 5-spiracle on metathorax; (D) abdominal lateral spiracular complex; 1-spiracle, 2-verruciform sensillum; (E) posterior spiracular plate; 1-minute acanthae, 2-rima, 3-interspiracular process; (F) stelix sensillum; 1-basal, conical, minute acanthus.

gan of the third instar of *N. appendiculata* (Fig. 4B-9) was not seen clearly enough to allow comparison with other species; however, the third instars of all five species of *Neaspilota* examined to date have oral ridges with dentate ventral margins characteristically arranged in vertical series ventrolaterad of the dorsal sensory organ and laterad of the oral cavity. Similar oral ridges also were described in the second instars of *N. viridescens* (Goeden and Headrick 1992), *N. wilsoni* (Goeden and Headrick 1999), and *N. signifera* (Goeden 2000a). The oral ridges number seven or eight in the third instar of *N. aenigma* (Goeden 2000b), seven in *N. appendiculata* (Fig. 4B-8), but six in the second and third instars of the other three congeners examined to date. The appearance and arrangement of these oral ridge appears to be a generic character; however, the present study confirms that the oral ridges vary in number among *Neaspilota* species. The third instars of *Trupanea imperfecta* (Coquillett), *T. jonesi* Curran, *T. nigricornis* (Coquillett), *T. pseudovicina* (Hering), *T. signata* Foote, and *T. wheeleri* Curran also bear serrated oral ridges (Goeden and Teerink 1997, 1998, 1999a; Goeden et al. 1998; Knio et al. 1996; Teerink and Goeden 1999), but these oral ridges appear to be fewer in number, and are not arranged in a more or less regular, vertical row laterad to the oral cavity, as in *Neaspilota*.

The mouth hooks of the third instars of *N. appendiculata*, *N. aenigma*, *N. signifera*, and *N. viridescens* are tridentate (Goeden and Headrick 1992; Goeden 2000a, b); whereas, those of the third instar of *N. wilsoni* are bidentate (Goeden and Headrick 1999). Such interspecific differences in dentation are supported by our findings that the mouth hooks of third-instar *Trupanea vicina* are bidentate; whereas, those of 12 other congeners examined from California are tridentate (Goeden and Teerink 2000b and citations therein).

The number and appearance of the stelex sensilla surrounding the posterior spiracular

plate differ among the *Neaspilota* species examined to date. These number only four in the first instars of *N. wilsoni* (Goeden and Headrick 1999). *N. aenigma* (Goeden 2000b), and *N. appendiculata*, but unfortunately were not observed with *N. signifera* (Goeden 2000a). This count of stelex sensilla remains at four in the second instars of *N. aenigma* (Goeden 2000b) and *N. appendiculata*, but increases to six in third instars of *N. wilsoni* (Goeden and Headrick 1999), *N. aenigma* (Goeden 2000b), and *N. appendiculata*. These stelex sensilla also show inter-instar (intraspecific) and interspecific differences in the incidence and appearance of the minute acanthae that ring them basally, but this was not recognized, studied or recorded by my coworkers and me until recently (Goeden 2000b and above description).

Puparium: Mostly pale yellow, with posterior two-three segments grayish to blackened, reniform, and smoothly rounded at both ends (Fig. 5A); anterior end bears the invagination scar (Fig. 5B-1) and anterior thoracic spiracles (Fig. 5B-2); caudal segment circumscribed by minute acanthae; three stelex sensilla, dorsolaterad, laterad, and ventrolaterad of posterior spiracular plates; posterior spiracular plate bears three broadly elliptical rimae (Fig. 5C-1), and four interspiracular processes, each with three to four branches (Fig. 5C-2); intermediate sensory complex with a medusoid sensillum and a stelex sensillum. Eleven puparia averaged 3.5 ± 0.08 (range, 3.13–3.84) mm in length; 1.51 ± 0.03 (range, 1.42–1.71) mm in width.

DISTRIBUTION AND HOSTS

Freidberg and Mathis (1986) described the distribution of *N. appendiculata* as, "Widespread in western United States between 32° and 46° north latitude and between 104° and 118° west longitude." Foote et al. (1993) mapped the distribution to include two or more collection records each from Arizona, Nevada, New Mexico, Utah, and Wyoming, along with additional single

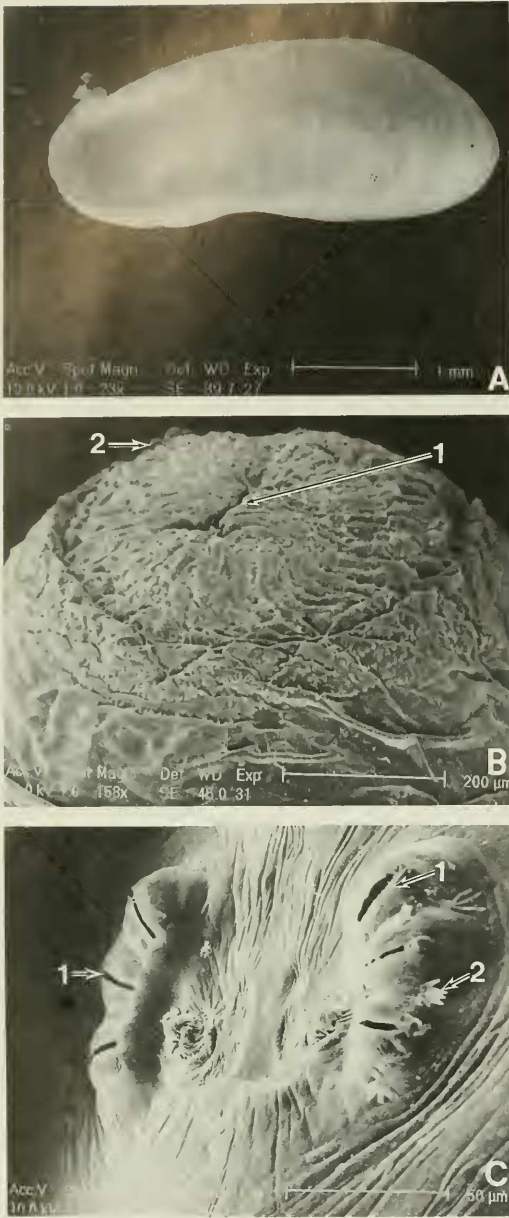


Fig. 5. Puparium of *Neaspilota appendiculata*: (A) habitus, anterior to left; (B) anterior end, 1—invagination scar, 2—anterior thoracic spiracle; (C) caudal segment, 1—rima, 2—interspiracular process.

collection records from California and Idaho, and a "state record only" from Colorado. Besides our three study sites, two other collection sites in California were along Pine Creek Road at 1774-m elevation, Inyo Nat. Forest, Inyo Co., 10.x.1990, and

Mountain Pass, S of Interstate Highway I-15 at 1369 m, E. San Bernardino Co., 6.11.1998.

The only reported and confirmed host plant of *N. appendiculata* is *Machaeranthera canescens* (Goeden 1989), belonging to the subtribe Solidagininae of the tribe Astereae in the family Asteraceae (Bremer 1994). This herbaceous, annual to short-lived perennial, host-plant species has at least five distinct varieties and itself is widely distributed in many habitats throughout western United States and into adjacent Canada and Mexico (Hickman 1993, Shreve and Wiggins 1964). Therefore, *N. appendiculata* provides still another apparent example of a true monophage reported among the nonfrugivorous Tephritidae (Headrick and Goeden 1998).

BIOLOGY

Egg.—In 16, mostly closed, preblossom, immature flower heads of *M. canescens*, 35 eggs were inserted pedicel-last, six (17%) with their long axis at a slight angle to the receptacle, and 29 (83%) with their long axis perpendicular to the receptacle. These 16 flower heads each contained an average of 2.2 ± 0.4 (range, 1–7) eggs. Three (9%) eggs were inserted between the phyllaries and outer ovules and 32 (91%) within single florets; 12 (34%) of the 35 eggs were inserted into corollas of peripheral florets and 20 (66%) into corollas of central florets. The diameters of the receptacles of these flower heads containing eggs averaged 2.4 ± 0.14 (range, 1.58–3.7) mm.

Larva.—Upon eclosion, the first instars usually tunneled into an ovule, or into a corolla before entering the ovule to which it was basally attached. Single first instars were found feeding within each of six, closed, preblossom or open flower heads. The receptacles of these flower heads averaged 2.4 ± 0.2 (range, 1.6–2.9) mm in diameter. An average of 3.3 ± 1.0 (range, 2–8) ovules of soft achenes was damaged in these six heads as the first instar tunneled into the layer of ovules or soft

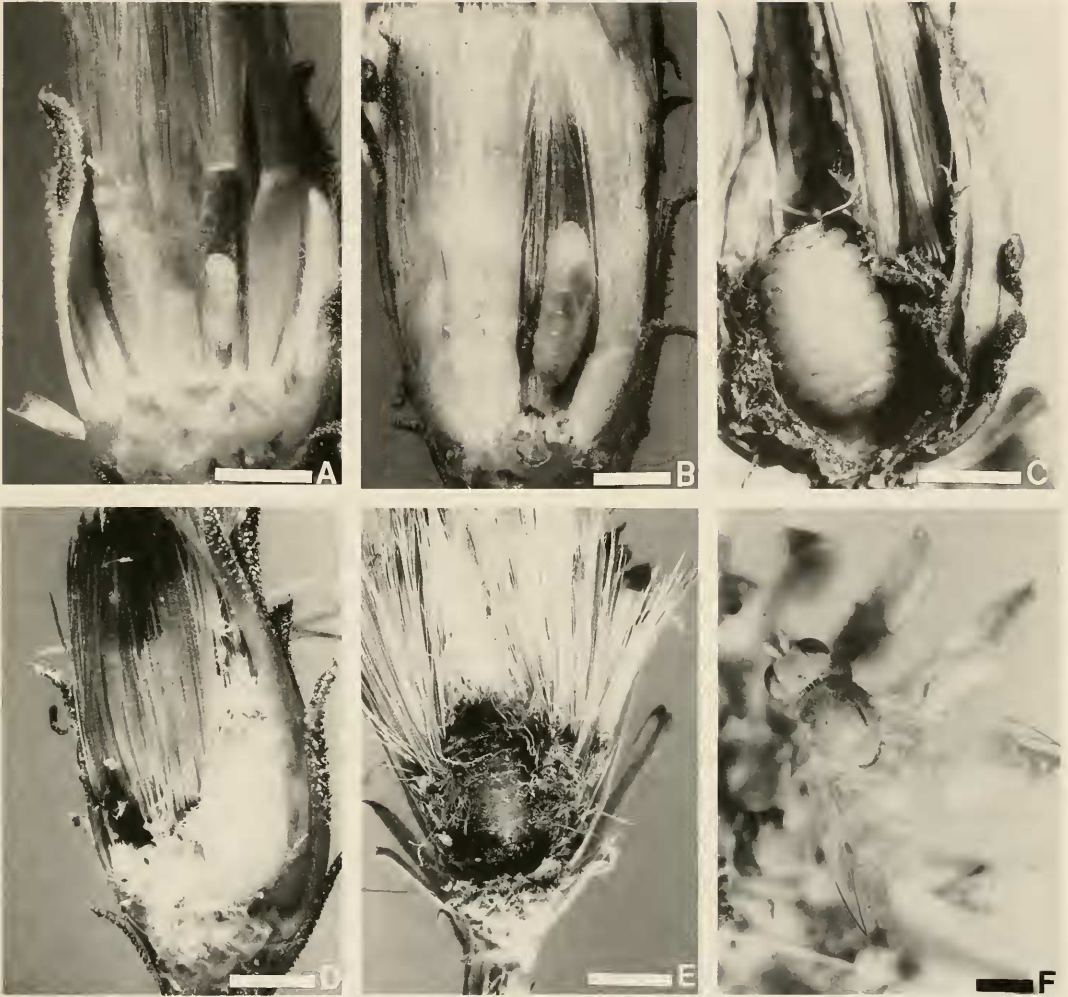


Fig. 6. Life stages of *Neaspilota appendiculata* in *Machaeranthera canescens*: (A) second instar feeding on soft achenes in open flower head, (B) third instar feeding on soft achenes in open flower head, (C) prepuparium in center of flower head, (D) puparium of nondiapausing individual formed in flower head in summer, (E) puparium formed in spring by overwintered prepuparium in flower head, (F) adult male. Lines = 1 mm.

achenes and parallel to and above the receptacle. No receptacles within these six infested flower heads were abraded or pitted by feeding. Based on 54 (range, 20–75) as the average total number of ovules and achenes, respectively, counted in 29 preblossom to postblossom flower heads, about 6% (range, 4–15%) of the ovules in the six infested, preblossom flower heads were damaged by first instars.

Second instars continued feeding on ovules in preblossom flower heads or in soft

achenes in open, blossom and post blossom, flower heads (Fig. 6A). All fed within a series of adjacent ovules/soft achenes with their bodies horizontal to and their mouthparts directed towards the receptacles, but always well above the receptacles. Receptacles of 14 flower heads containing second instars were not fed upon and averaged 2.94 ± 0.29 (range, 1.99–5.7) mm in diameter. These flower heads each contained an average of 1.2 ± 0.2 (range, 1–3) larvae that had destroyed an average of 10.3 ± 2.1

(range, 2–31) ovules/soft achenes, or as calculated for the preceding instar, about 19% (range, 4–57%) of the average total of 54 ovules/soft achenes per flower head.

Third instars initially continued to feed mainly on soft achenes in post blossom flower heads; however, prior to pupariation, and usually before all the achenes were damaged, they proceeded to tunnel into the center of the receptacle (Fig. 6B). Sixty-five flower heads that averaged 3.09 ± 0.14 (range, 1.71–7.19) mm in diameter each contained a single third instar, so intraspecific mortality occurs in heads containing more than one larva. An average of 51 ± 7.1 (range, 24–63) of the soft achenes therein were damaged, or about 94% (range, 44–100%) of the average total of 54 ovules/soft achenes per flower head. These percentages of seed predation per larva per flower head are on the high side among florivorous tephritids studied by us to date (Headrick and Goeden 1998); this seed predation was exceeded only by gregarious florivorous species like *Trupanea conjuncta* (Adams) (Goeden 1987) and *T. pseudovicina* Hering (Goeden and Teerink 1998) or by species with large larvae that develop in immature or small flower heads like *Paracantha cultaris* (Coquillett) (Cavender and Goeden 1984) and *Xenochaeta dichromata* Snow (Goeden and Teerink 1997).

Third instars in flower heads fed with their long axes oriented perpendicular to and mouthparts directed towards the receptacles (Fig. 6B). Ninety percent of the third instars in the 65 infested heads scored or pitted the receptacles and thus presumably supplemented their diet with sap. Goeden and Headrick (1992, 1999) described and discussed this similar type of feeding by *N. viridescens* and *N. wilsoni*. And, as also reported for both of these congeners (Goeden and Headrick 1992, 1999), most third instars became surrounded for about 90% their lengths by cells, which occupied most of the interior of the flower heads and consisted of ovule-, achene-, chaff-, papus-, and corolla-fragments cemented to-

gether by liquid feces and sap that hardened when dry (Fig. 6C). These protective cells were slightly larger than the mature larva, externally incorporated the outer walls of achenes and the few uneaten achenes, and were blackened and smooth inside. Upon completing feeding and cell construction, the third instars oriented with their anterior ends towards the receptacles, retracted their mouthparts, and formed prepuparia (Headrick and Goeden 1998). Most individuals overwintered in diapause as prepuparia (Fig. 6C) (Goeden and Headrick 1992, 1999; Headrick and Goeden 1998), but a few individuals pupariated early and emerged in late-summer and fall (August–September) (Fig. 6D). Prior to pupariation the prepuparia reversed their orientation within their cells and turned 180° such that their heads were directed away from the receptacles (Fig. 6D, E).

Pupa.—The receptacles of 11, overwintered, postblossom flower heads, each also containing a single puparium (Fig. 6E), averaged 3.50 ± 0.08 (range, 3.13–3.84) mm in diameter.

Adult.—Adults emerged from overwintered, mature flower heads, and were long-lived under insectary conditions, as 24 unmated males (Fig. 6F) averaged 64 ± 9 (range, 10–177) days, and 14 virgin females averaged 73 ± 12 (range, 10–133) days. Such lengthy longevities compare favorably with average adult longevities reported for adults of *N. viridescens* (Goeden and Headrick 1992), *N. wilsoni* (Goeden and Headrick 1999), *N. signifera* (Goeden 1999a), and *N. aenigma* (Goeden 1999b).

The premating and mating behaviors of *N. appendiculata* were not studied in the field, but were observed in petri dish arenas found to be so useful with many other non-frugivorous tephritid species (Headrick and Goeden 1994). Premating behaviors observed with paired *N. appendiculata* (n) were brief “kissings” (n = 2), side-stepping by males while tracking females (n = 4) (Headrick and Goeden 1994), and rapid wing hamation, sometimes combined with

lofting about 20° by both sexes ($n = 6$) (Headrick and Goeden 1994). Two matings were observed that began during late afternoon in twilight involving different pairs of flies that lasted 225 and 345 min. These compared to average durations of 190 min reported for *N. aenigma* (Goeden 2000b), 235 min. reported for *N. wilsoni* (Goeden and Headrick 1999), 238 min. reported for *N. signifera* (Goeden 2000a), and 5.3 h reported for *N. viridescens* (Goeden and Headrick 1992). No post-copulatory behavior reminiscent of the mate guarding observed with *N. signifera* (Goeden 2000a), *Dioxya sororcula* (Wiedemann) (Headrick et al. 1996), and *Euaresta stigmatica* Coquillett (Headrick et al. 1995) was observed with *N. appendiculata*. Postcopulatory behavior by *N. appendiculata* mainly consisted of storing of genitalia by males and cleaning and grooming by both sexes (Headrick and Goeden 1994).

Seasonal history.—The life cycle of *N. appendiculata* in southern California follows an aggregative pattern (Headrick and Goeden 1994, 1998) in which the prepuparium is the principal overwintering stage. Come late spring (April–May), overwintered prepuparia reverse their orientation in their cells in flower heads on shoots of dead host plants and pupariate. Adults emerge during May and June and aggregate on preblossom shoots of *M. canescens* to mate. Females oviposit in the small, newly-formed, closed, preblossom flower heads in June and July and larvae feed until fully grown, then enter diapause in the late summer and early fall (August–October). There is a single generation per year on their sole host plant, although as mentioned above, a few adults emerge in August–September, perhaps to produce a partial generation on late-flowering plants, or to overwinter as long-lived adults.

Natural enemies.—Two males and two females of *Pteromalus* sp. (Hymenoptera: Pteromalidae) were reared from separate puparia of *N. appendiculata* as solitary, larval-pupal endoparasitoids. Seven, 15, and

17 individuals of an unidentified Eulophidae (Hymenoptera) respectively were reared from three puparia as gregarious endoparasitoids.

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